CHAPTER 14

HISTORICAL CONTINGENCY AND LIZARD COMMUNITY ECOLOGY

Jonathan B. Losos

Community ecologists usually focus on the following questions: (1) What processes are operating within a community? (2) What processes led to the currently observed structure of a community? (3) What accounts for the differences and/or similarities among communities?

Although the first question concerns what is happening within present-day communities, the latter two questions inquire about the processes responsible for patterns observed in extant communities. These latter questions directly address the historical genesis of community patterns: through what route and guided by what processes have communities attained their current state? Such questions are critical to investigation of present-day community patterns for several reasons. On one hand, observed patterns often could be the result of a number of different processes (Case and Sidell 1983). Conversely, the same process can lead to different end-states whether starting conditions are identical or not (Drake 1990, 1991; Drake et al. 1993). Consequently, often it is not possible to draw inferences about the processes that shaped a community solely from inspection of the current structure of that community; what is needed is information on how a community came to its current state (Ricklefs 1987; Brooks and McLennan 1991; Losos 1992; Gorman 1993).

Recent years have seen widespread acceptance of the idea that historical phenomena must be studied in an explicitly historical context (Lauder 1982; Cracraft 1990; Harvey and Pagel 1991; Brooks and McLennan 1991). Ecologists have long been aware that historical contingencies may be responsible for differences among communities, but analyses of historical ecology have generally looked to the history of the environment for explanation (Ricklefs 1987). Examples include enhanced speciation in forest refugia as a cause of tropical diversity (e.g., Haffer 1969) and oceanic islands having lower species richness than continental islands because the former were never connected with the mainland (e.g., Case 1975; Wilcox 1978).

A complementary approach that incorporates historical information into ecological analyses considers the history of the taxa that make up a community (e.g., Duellman and Pianka 1990). In some cases, the fossil record is sufficient to permit inferences about paleo-community structure and processes (e.g., Russell 1991; Warheit 1992), but a more generally applicable method is to examine the phylogeny of lineages present in a community.

A phylogenetic perspective can permit insight about the diversification and evolutionary changes that have occurred and resulted in the currently observed community. Further, comparison of lineages in multiple communities can provide insight into the causes of differences and similarities among communities (e.g., Brooks and McLennan 1991; Cadle and Greene 1993).

Lizards have played a key role in the development of community ecology theory. To name just a few examples, studies of lizard communities have been important in the formulation of ideas concerning species diversity (Vanzolini and Williams 1970; Pianka 1972), island biogeography (MacArthur and Williams 1967; Schoener 1970; Case 1975, 1983), resource partitioning (Schoener 1968b; Pianka 1969b), niche complementarity (Pianka 1973; Schoener 1974), competition (Dunham 1980; Pacala and Roughgarden 1985), and predation (Schall and Pianka 1980). Here, using lizard communities as an example, I discuss and review how phylogenetic information can be integrated into studies of community ecology.

The Role of History in Determining Community Structure

Species diversity

Ecologists have long been interested in why some communities have more species than others. Species diversity is a function of two factors: the pool of available species and the number of species that the community can contain. Most theories emphasize the latter aspect and investigate proximate ecological factors as an explanation for the diversity of a community. However, if communities are not saturated, then species diversity could also be a function of the number of species potentially available to join the community–the larger the regional pool of species, the greater the diversity of local communities (MacArthur 1965; Ricklefs 1987). The size of the pool of available species, which includes all species within a community plus all other species physically capable of immigrating into the community, is ultimately determined by rates of extinction and speciation. Because lineages differ in their propensity to speciate or perish, the pool of available species may differ as a result of among-region differences in which lineages are present. These differences, in turn, may result in differences in local diversity.

Variation in local diversity also may result from historical contingency. Hypotheses that look to proximate ecological conditions as an explanation for differences in diversity assume that the ecological "types" of species available in the species pools of different communities are comparable. But if certain "types" are not present in a pool for whatever reason (e.g., random extinction, constraint on the evolution of appropriate phenotype in lineages

present in the species pool), then the "niche" normally utilized by that type may not be filled in a given community (e.g., Pianka 1989, p. 354).

Examination of the lineages present in different communities can allow an assessment of how important historical factors may be in contributing to observed patterns. As an example, I will consider differences in species richness of desert lizard communities based on the data of Pianka (1986). Pianka and colleagues have demonstrated that the number of lizard species inhabiting desert communities varies remarkably among continents, from as few as four in North American deserts to as many as 42 in Australian deserts (Pianka 1986; see Table 14.1).

How can this difference in diversity be explained? A variety of proximate explanations have been advanced: lizards have replaced snakes and mammalian carnivores in Australia; fewer nonlizard competitors and predators are present in the more diverse communities; resource levels (e.g., low fertility of soils makes deserts inhospitable to endotherms) or habitat structure differs among continents (reviewed and discussed in Pianka 1986, 1989; Morton and James 1988). Alternatively, we must entertain the possibility that the history of the deserts themselves is responsible for differences in diversity. Perhaps climatic conditions have promoted speciation in Australian deserts but not in North American deserts (discussed in Cogger 1984; Pianka 1986), or perhaps Australian deserts are considerably older than North American deserts (Pianka 1986).

An alternative hypothesis recognizes that different lizard lineages occur in the deserts of North America and Australia and suggests that the disparity in species richness results from interlineage variation in the propensity to survive and speciate. Consider the lizard families present in Australian and North American desert communities (Table 14.1). Five families are present in each, but only one, the Gekkonidae, is found in both (although no skinks occurred at Pianka's North American study sites, two skink species extend their ranges to include relictual mesic and/or rocky habitats in some North American deserts [Stebbins 1985; Greene pers. comm.; Vitt pers. comm.]). Further, among the Gekkonidae, all Australian geckos are members of the diplodactyline, gekkonine, and pygopodine lineages, whereas North American taxa belong to the Eublepharinae (Kluge 1987), with the exception of one species that occurs in extreme southwestern North America (Stebbins 1985). Consequently, an alternative hypothesis is that the lineages in Australia are intrinsically more prone to speciate and/or coexist than those in North America, perhaps for reasons unrelated to proximate differences in the deserts of the two continents.

Is this a reasonable alternative hypothesis? Comparison of the lineages present on the two continents indicates that the lineages present for Australia's great diversity are absent in North America, whereas lineages present in

Table 14.1. Comparison of the lizard fauna of Australian and North American deserts (numbers below are the range, with the mean, when available, in parentheses; data from Pianka 1986).

	North America	Australia
Total Species Number	4–11 (7.4)	18–42 (29.8)
Species Number by Family		
Agamidae*	0	2–8
Gekkonidae	1	5–9
Helodermatidae	1	0
Iguanidae†	3–8	0
Pygopodidae	0	1–2
Scincidae	0	6–18
Teiidae	1	0
Varanidae	0	1–5
Xantusiidae	1	0
Species Number by Habits		
Nocturnal	0–2 (1.0)	8–13 (10.2)
Arboreal	0–3 (0.9)	1–9 (5.4)
Fossorial	0 (0)	1–2 (1.2)

* In the taxonomy of Frost and Etheridge (1989), Agamidae is now considered a subfamily (Agaminae) of the Chamaeleonidae.
† In the taxonomy of Frost and Etheridge (1989), the families represented would be Crotaphytidae, Iguanidae, and Phrynosomatidae.

North America but not Australia tend not to radiate. The three families responsible for Australia's heightened diversity are the Varanidae, Scincidae, and Gekkonidae (including pygopodids). The Varanidae are currently restricted to the Old World, the one gekkonid lineage in North American deserts is not speciose anywhere in its range (Grismer 1988), and skinks barely occur in North American deserts (see above). Thus, one would not have expected these lineages to have contributed substantially to North American desert diversity. By contrast, two families found in North America and not in Australia, the Helodermatidae and Xantusiidae, are both depauperate in species (2 and 19 species respectively) and fail to compensate for the lineages absent from North American deserts. A third family that occurs in North American deserts is the Teiidae. Although teiids have diversified in the tropics of Central and South America, their diversity in deserts of North and South American deserts is relatively low (see Peters and Donoso-Barros 1970; Stebbins 1985). Finally, North American iguanians and Australian

iguanians (referred to as Agamidae here, but considered a subfamily [Agaminae] of the Chamaeleonidae by Frost and Etheridge 1989), which may be considered broadly as ecological analogues, are approximately equal in diversity in deserts on the two continents (note that the Iguanidae has been split into eight families by Frost and Etheridge 1989, three of which are found in North American deserts).

One could thus interpret differences in diversity in two ways. On one hand, one might argue that lizard families do not intrinsically differ in speciation or extinction rates and only ecological factors regulate how many species can coexist. On the other hand, differences in diversity may be a function of intrinsic properties of the lineages present on the two continents and unrelated to proximate environmental effects. Perhaps some lineages are more prone to speciate or less susceptible to extinction than others (perhaps as a result of interlineage differences in population density or substructuring, levels of gene flow, or type of species-recognition signal). Alternatively, some lineages intrinsically may be more capable of partitioning resources more finely than others, as Pianka (1972) suggested for Australian skinks.

To make these possibilities more concrete, consider what postulates are implicit in the view that differences in desert-lizard diversity result from proximate ecological causes: (1) New world skinks and/or teiids are the ecological analogues of Australian skinks and would have diversified to an equal extent if they had originally occurred in Australian deserts, even though their diversity is low in North American deserts. Equivalently, one would contend that had Australian skink lineages occurred in North American deserts, they would not have radiated. (2) Eublepharine geckos, which are nowhere speciose (only 5 genera and 22 species worldwide; Grismer 1988), would have radiated widely and into arboreal niches in Australia; similarly, arboreal Australian geckos would not have diversified in North America. (3) Varanids would not be able to survive or proliferate in North America. (4) Helodermatids and xantusiids would possibly have radiated in Australia.

These points suggest a reappraisal of the conclusion that differences in diversity result from environmental differences between deserts. Certainly, some of the differences between Australian and North American deserts are due to ecological differences among the sites. For example, one large difference is the number of arboreal species per community ($\bar{x}$ = 5.4 in Australia, 0.9 in North America; Pianka 1986), which has been attributed to the greater availability of trees in Australian deserts (Pianka 1986, 1989; Morton and James 1988). Occupation of the arboreal niche has occurred in four Australian families (Agamidae, Gekkonidae, Scincidae, Varanidae). Consequently, it is clearly an adaptive shift undertaken repeatedly in response to environmental conditions, rather than a result of the inherent tendencies of a single lineage.

By contrast, other aspects of the difference in diversity could have resulted from historical contingency. Much of the difference in species richness between Australia and North America results because Australia has considerably more nocturnal, carnivorous (sensu stricto), fossorial, and skink-like species. I suggest the possibility that this is a function of the lineages present in each continent rather than a consequence of environmental differences among continents.

The disparity in the number of nocturnal species ($\bar{x}$ = 10.2 in Australia, 1.0 in North America; Pianka 1986) is almost completely the result of the occurrence of the Gekkonoidea (sensu Kluge 1987) in Australia and the Eublepharinae in North America. Gekkonoids are both speciose and ecologically diverse throughout their range; eublepharines are neither. Ecological explanations of differences in the number of nocturnal species that are particular to differences in deserts on these continents thus appear too narrowly focused (see also Cogger 1984).

Similarly, why is there a paucity of carnivorous and fossorial lizards in North America? Ecological explanations (e.g., lack of resources, competition from other taxa) are certainly possibly correct. But one also must entertain the possibility that lineages present in North America are not capable of producing such forms. In South America, several genera (*Callopistes, Tupinambis*) within the Teiioidea (sensu Estes et al. 1988) have evolved that are superficially similar to varanids; other Teiioidea (e.g., *Bachia*) have moved toward fossoriality by becoming elongate with reduced limbs. Thus, one could argue that the Teiioidea, as represented in North America by *Cnemidophorus*, has the potential to attain morphologies and ecologies similar to those exhibited in Australia. On the other hand, the closest relatives of *Cnemidophorus* (the *Ameiva* species group: *Ameiva, Teius, Kentropyx*, and *Dicrodon*; Gorman 1970; Presch 1983) vary little morphologically despite occurring in a wide range of habitats (e.g., Vitt and Carvalho 1992), which might suggest that North American *Cnemidophorus* do not have the evolutionary potential to fill carnivorous or fossorial niches (however, the *Ameiva* group of macroteiids does vary in dental morphology and diet; Presch 1974). Iguanians, which are considerably more diverse than teiids in North America, show no tendency anywhere toward fossoriality and only a limited trend toward an analogue to varanids (*Crotaphytus, Gambelia*). Thus, it is not clear whether the lack of carnivorous and fossorial lizard taxa in North America is due to lack of ecological opportunity or to internal constraints preventing the production of such forms in North American iguanian and teiid lineages.

Finally, why has no radiation comparable to the Australian skinks occurred in North America? The closest ecological analogue to Australian skinks is again *Cnemidophorus*. In some areas, not included in Pianka's

study sites, as many as five species of *Cnemidophorus* co-occur (Wright and Vitt 1993), but nowhere does this genus display the ecological or morphological diversity of Australian skinks, even when nonskink-like genera (e.g., *Lerista*) are excluded.

The bottom line is that lack of adaptive radiation in teiids, as represented by *Cnemidophorus*, and geckos, represented by *Coleonyx*, is responsible for the low diversity in North America. Certainly, it is conceivable that these taxa have the capability to speciate and radiate, and had they been in Australia, they would have produced a radiation comparable to that displayed by Australian taxa. But the other possibility is that, due to particular quirks of these lineages, they have not radiated, for reasons possibly completely unrelated to the proximate conditions of their surroundings. Perhaps their population biology is such that speciation rarely occurs? Perhaps they are so highly specialized and constrained that major morphological change (e.g., limb loss, evolution of toe-pads; eublepharines exhibit few subdigital specializations; Grismer 1988) is not permissible?

These possibilities are difficult to investigate. However, posing the questions can lead to an important reorientation of the focus of research. Questions of speciation and morphological constraint require population genetic and evolutionary approaches. Only by integrating these approaches with ecological comparisons of community structure can we address questions such as those posed above. More broadly, the point is that there often will be plausible explanations for differences in diversity among communities. By ignoring historical phenomenon, one implicitly makes a variety of assumptions, some of which are reasonable, others less so. Almost certainly, both historical and ecological factors are always important in determining diversity (Duellman and Pianka 1990).

Ironically, although large scale intercontinental comparisons allow us to examine independent radiations and allow a comparative approach, they also come with a drawback. If all deserts had equal numbers of species, we would accept this as evidence for ecological regulation of species diversity. But when differences arise, there will always be the problem of confounding variables, the presence of different lineages in different communities. Thus, in this respect, intracontinental comparisons may be more compelling because the same lineages are present in each community.

Community structure

The current structure of a community is the result not only of processes currently operating, but also of those that shaped the community during its genesis. Because the same pattern could be produced by several, often quite distinct, processes, inferring process from pattern can be problematic (Case and Sidell 1983; Drake 1990).

Phylogenetic analyses can be useful in distinguishing possible explana-
tions for observed patterns. An example is the cause of nonrandom size-
structuring in communities. Many authors have suggested that species in a
community differ more in body size (a presumed indicator of resource use)
than expected by chance (Schoener 1986b; Dayan et al. 1990; Taper and
Case 1992; and references therein). Although numerous processes could
produce such a pattern, they can be divided into two categories: ecological
and coevolutionary theories. Ecological theories assume that there is a
potential source pool of species varying in size, but the only species that can
colonize a community are those that are sufficiently different in size from
species already present. Coevolutionary explanations suggest that size evolu-
tion occurred subsequent to sympatry. Coevolution could take the form of
divergence (= character displacement), convergence, or parallel directional
evolution (e.g., Schoener 1970; Roughgarden and Pacala 1989; Abrams
1990; and references therein). Processes responsible for either ecological
sorting by size or coevolution (size assortment and size adjustment; sensu
Case and Sidell 1983) include interspecific competition, predation, and
interspecific hybridization.

Case and Sidell (1983; see also Case 1983) proposed the first test to dis-
tinguish between the two processes. They suggested comparing all possible
sets of sympatric species to those sets that actually occur (e.g., in an archi-
pelago, compare all possible 3-species communities to those 3-species com-
munities that actually exist). If size assortment has occurred, then species in
real communities should be more different in size than would be expected
from the set of all possible communities. By contrast, tests for coevolution
(termed "size adjustment" by Case and Sidell 1983) compare the difference
in size between sympatric species against all possible combinations of popu-
lations of these species. The expectation is that populations of generally
similar-sized species will be under much greater selective pressure to
diverge in size when sympatric than will populations of species that are not
generally similar in size. Thus, the more similar two species are in size, as
judged by all possible combinations of populations of the two species, the
more greatly divergent the two sympatric populations should be. Case
(1983) used this protocol to investigate patterns of size distributions in
Cnemidophorus assemblages.

Although this method is implicitly phylogenetic, by comparing popula-
tions to their close relatives, a more directly phylogenetic approach might be
preferable when possible. I suggested such an approach to analyze
size-structured communities in Lesser Antillean *Anolis* lizards (Losos
1990a,b). In the northern Lesser Antilles, five of six two-species islands con-
tain a large and a small species, and 10 of 11 one-species islands contain an
intermediate-sized species (Schoener 1970). I predicted that if character
displacement were responsible for this pattern, then phylogenetic character

reconstruction should indicate that size change occurred coincidentally with the attainment of sympatry of two previously similar-sized taxa. Phylogenetic analysis indicated exactly this pattern, but also suggested that character displacement may have occurred only once (Fig. 14.1). Consequently, character displacement is probably responsible for the evolution of different-sized species which are capable of coexisting, but the occurrence of pairs of dissimilar-sized species on five islands must be the result of size assortment. Thus, the phylogenetic analysis not only indicates that both processes probably have been operating, but also gives some indication of their relative importance.

In a similar vein, Arnold (1981, 1990, 1993) used a phylogenetic approach to understand differences in habitat use among various lizard clades. A number of lacertid and gekkonid clades display a trend in which more derived taxa progress along a continuum, using and adapting to increasingly more environmentally challenging habitats (often xeric habitats; Fig. 14.2). Arnold suggested that this pattern results from competitive pressures, which force newly arisen taxa to utilize marginal and previously nonutilized niches. Speciation in these taxa, in turn, leads to taxa that must shift into even more marginal niches to avoid competitive exclusion.

A second important role for phylogenetic analyses is in statistical comparative methods. Comparative analyses that ignore phylogenetic relationships are invalid because they assume that the character value of each species is independent of the value of all other species (e.g., Felsenstein 1985; Harvey and Pagel 1991). A variety of statistical methods has been proposed to incorporate phylogenetic information into statistical analyses (reviewed in Harvey and Pagel 1991; Losos and Miles 1994; see also chapters by Garland and Martins this volume).

Reconstruction of community evolution

Phylogenetic methods allow one to trace a community's historical development. Such reconstructions can reveal patterns and suggest hypotheses not apparent from consideration of the structure of extant communities.

One reasonably well-understood example involves communities of *Anolis* lizards in the Greater Antilles, which are very similar in composition. This convergence has resulted from the evolution of the same set of "ecomorphs" on each island (Williams 1983). Phylogenetic analysis of the anole radiations on Puerto Rico and Jamaica revealed that not only are extant communities convergent in structure, but they attained their current state by passing through essentially the same set of intermediate community structures (Losos 1992; Fig. 14.3). As discussed above, many processes can produce similar patterns in present-day communities; consequently, only an historical analysis could present evidence for an hypothesis of parallel community evolution.
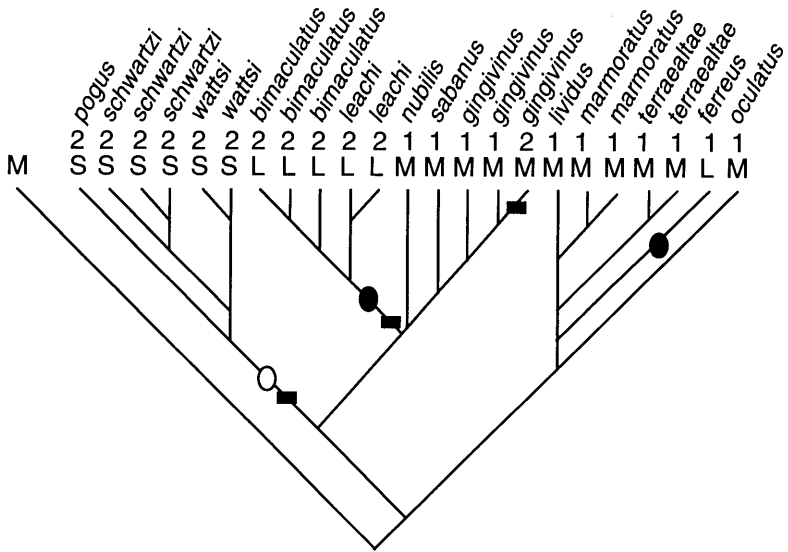
Figure 14.1. Evolution of body size in *Anolis* lizards of the northern Lesser Antilles (based on Roughgarden and Pacala 1989 and Losos 1990a,c). Numbers indicate the number of *Anolis* species on the island occupied by each taxon. Letters indicate body size (small, medium, or large). Circles represent major evolutionary changes in body size (solid = increase; open = decrease); bars represent the transition from an ancestor on a one-species island to a descendant on a two-species island. The statistical analysis in Losos (1990a,c) used actual values rather than categorical variables. Figure redrawn from Losos (1992) with permission.
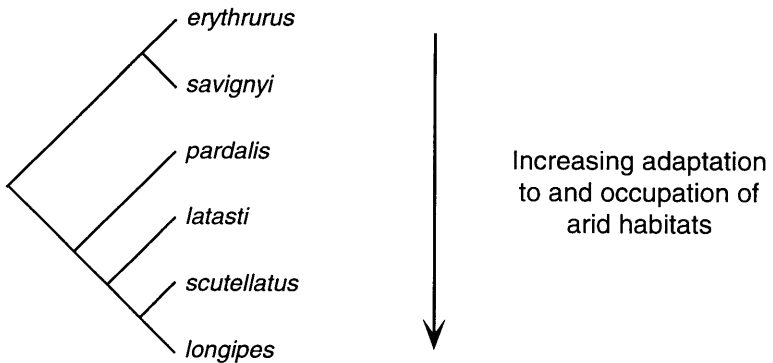

Figure 14.2. Evolution of *Acanthodactylus* in northern Africa near the Sahara. Modified from Arnold (1981).
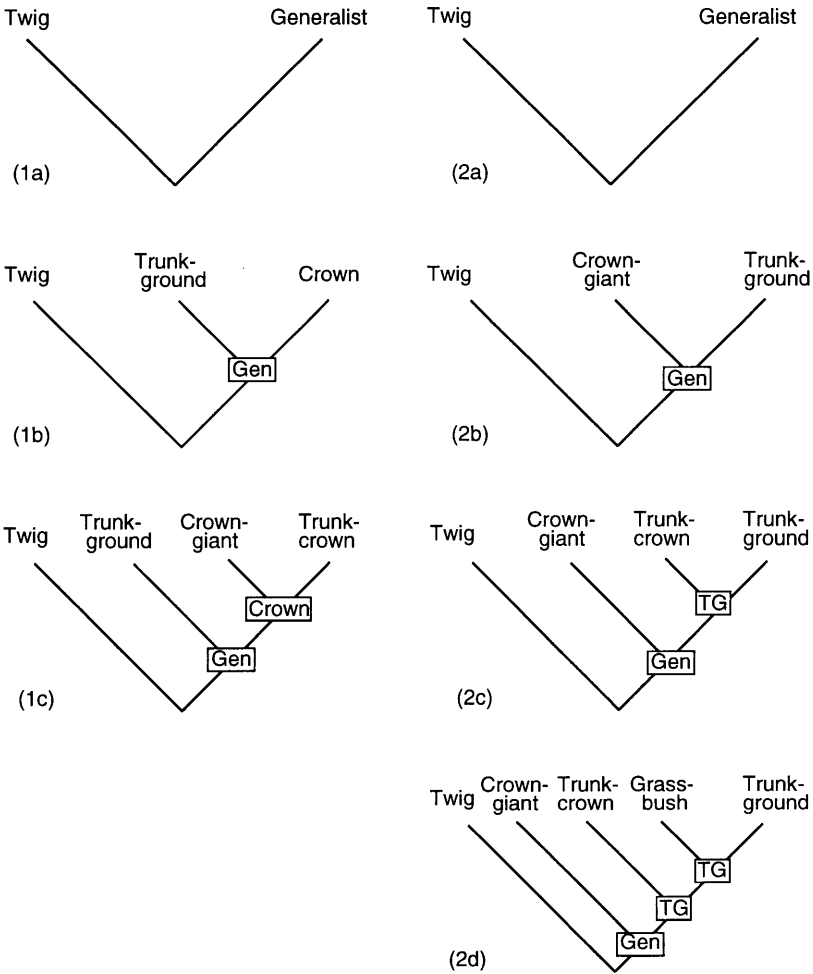
Figure 14.3. The evolution of *Anolis* community structure in (1) Jamaica and (2) Puerto Rico. Evolution of habitat use, as predicted by morphology, was reconstructed using parsimony methods (see Losos 1992 for methodological details). Not only are anole communities on the two islands very similar today (the only difference being the presence of grass-bush anoles in Puerto Rico), but the intermediate stages in community evolution on both islands were also quite similar. The names of the ecomorphs refer to the habitat they normally utilize. Redrawn with permission from Losos (1992).

Phylogenetic analysis provides an important additional perspective on anole community structure. Puerto Rico has five ecomorph types, whereas Jamaica only has four; the missing type in Jamaica is the "grass-bush" ecomorph. One might reasonably ask why the grass-bush niche is vacant in Jamaica, particularly because grassy areas exist in Jamaica and no other taxa obviously has usurped that ecological role. Phylogenetic analysis suggests that the wrong question is being addressed (Williams 1972; Losos 1992). The grass-bush ecomorph is the fifth, and last, type to have evolved in Puerto Rico. Thus, at the most proximate level, the reason the grass-bush ecomorph is absent in Jamaica is because it is the fifth type to evolve in the ecomorph radiation sequence, and Jamaica has only progressed to the four-ecomorph stage. Thus, the more appropriate question is not: Why do grass-bush anoles not occur on Jamaica? but, rather: Why has Jamaica only made it to the four-ecomorph stage? The answer may have nothing to do with grass-bush anoles and their habitat, but may, instead, pertain to species-packing, rates of speciation, or age of the Jamaican radiation.

Discussion

I have argued that studies of community structure are incomplete if phylogenetic information is not considered. This view is part of a broader perspective that historical contingencies often play a large role in determining the composition of communities (Ricklefs 1987; Duellman and Pianka 1990; Cadle and Greene 1993). As is currently being recognized in all fields of organismal biology, historical analyses are an important complement to the study of function and structure of extant entities, be they organisms, taxa, or communities.

The application of phylogenetic principles to questions of community ecology will not always be straightforward, however, because community composition is a result of speciation, extinction, immigration, and in situ evolutionary change. Reconstructing the historical sequence of events in communities containing multiple lineages may prove particularly difficult because phylogenetic reconstructions within a lineage only provide information on relative order of branching. Thus, without supplemental information on the absolute timing of events (as might be provided by fossil material or molecular clocks, for instance), it may prove difficult to determine the relative ordering of either speciation events occurring in several lineages or of immigration and speciation events. In this respect, communities composed of monophyletic radiations, as often occurs on islands, may prove more tractable. On the other hand, in comparative community studies, it may be most beneficial to go to the other extreme and examine communities that contain multiple lineages present in each of the communities (e.g., Brooks and

McLennan 1991; Gorman 1993). While making it more difficult to recon-struct the precise sequence of events, this latter approach will avoid the problem of confounding differences in community structure with differ-ences in lineage characteristics (Losos and Miles 1994).

Importance of monophyly

Phylogenetic systematists stress the importance of only considering mono-phyletic groups (Brooks and McLennan 1991; Wiley et al. 1991). This rule makes sense for systematic and evolutionary studies, in which the study of paraphyletic groups (i.e., taxa that do not include all of the descendants of a common ancestor) can lead to mistaken inferences. However, as an absolute rule, this prescription is inappropriate for ecological studies. Most studies of community ecology, for example, consider a subset of the species present in a community that might be expected to interact with each other or the envi-ronment in a similar way (often termed a guild or assemblage; Terborgh and Robinson 1986). Guilds are not monophyletic units, but, rather, are often composed of members of a number of lineages. Further, monophyletic lin-eages often contain members of several guilds, particularly when some taxa have evolved substantially and have become ecologically distinct. For exam-ple, studies of mammalian communities often exclude bats because they have diverged to the extent that they interact with the environment in a completely different way than earthbound mammals. Thus, in determining which species to include in studies of community ecology, taxa should be categorized in an ecologically relevant fashion; such classifications will often not be completely concordant with phylogenetic classifications.

Reliance on current Linnean classification, which is based on a mixture of phylogenetic and morphological criteria, may be the worst choice, how-ever. For example, most phylogenetic analyses agree that snakes are most closely related to scleroglossan lizards; lizards, thus, are a paraphyletic group (Estes et al. 1988; Fig. 14.4). Many studies of lizard community ecology do not include snakes because they are morphologically, ecologically, and behaviorally quite distinct from "standard" lizards. However, excluding snakes is only legitimate if other legless and/or fossorial squamates are also excluded. The loss of limbs has evolved a minimum of 12 times in squa-mates, usually in association with cluttered, narrow, or fossorial habitats (Gans 1975; Gans et al. 1978; Edwards 1985; Shine 1986; Fig. 14.4). Thus, there is little justification, either ecologically or phylogenetically, for includ-ing most legless squamate lineages in studies of lizard community ecology because they are called lizards, but excluding one (snakes) because it has a different name. If ecological criteria (e.g., foraging mode, way-of-life, adap-tive zone) are used to delimit the boundaries of an ecological study, they must be applied to all taxa and not just certain lineages.
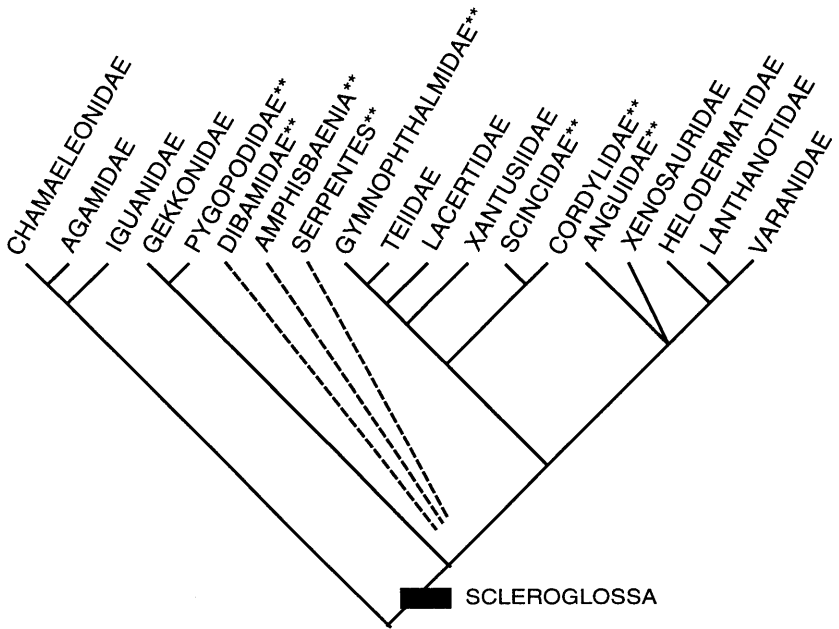
Figure 14.4. Phylogenetic relationships of squamates (following Estes et al. 1988). Dibamids, amphisbaenians, and snakes all lie within the Scleroglossa, but their position is unclear. Asterisks refer to taxa in which limb reduction has occurred in one or more lineages to the extent that limbs are functionally useless for locomotion.

Testing phylogenetically inspired hypotheses

In recent years, ecologists have emphasized the importance of experimentally testing hypotheses. Phylogenetic analyses pertain to the historical development of a community. These analyses describe historical patterns, from which inferences about processes can be drawn. Because such inferences are by necessity retrospective, they are not amenable to direct experimental testing. However, hypotheses derived from phylogenetic analyses often can be tested on extant taxa (Brooks and McLennan 1991; Losos and Miles 1994).

For example, analyses might suggest that competitive pressures led to character divergence. One could test this by experimentally placing two species together and investigating whether (1) competition occurs and, if so, whether (2) microevolutionary divergence occurs. Natural selection often can lead to rapid microevolutionary change (reviewed in Mayr 1963; Williams 1992; Losos et al. in press) so that such hypotheses could be tested in relatively short (in evolutionary terms) experiments. Similarly, hypotheses about differences in community structure could be examined by introducing

lineages from one community into another. For example, introduction of varanid lizards into North American deserts would permit one to test whether ecological or biogeographical factors are responsible for the absence of varanid-like forms there. Of course, such experiments can only ethically be performed in circumstances in which no long-term effects on the biota will occur. However, such experiments have already inadvertently been established in many areas through unintentional (at least from a scientific viewpoint) human-assisted introductions (e.g., Wilson and Porras 1983; Losos et al. 1993).

Phylogenetic information can be used to test hypotheses generated from ecological studies, as well as vice-versa. For example, based on studies of extant taxa, it could be concluded that a particular process, such as competition, is important. If evolutionary outcomes that this process should produce can be identified, then predictions testable by reference to a phylogeny can be generated (e.g., Arnold 1981; Gorman 1993).

Only rarely will ecological forces be so strong as to completely erase the vestiges of history. Thus, to fully understand the structure of extant communities will require a synthetic approach that conducts studies of ongoing processes in the context of historical patterns of community development and evolution.

Acknowledgments